THE DEATH-FEINTS OF SITOPHILUS GRANARIUS LINN., AND SITOPHILUS ORYZÆ LINN.

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The death-feigning instinct, which is well developed in many insects and which occurs frequently in many of the Coleoptera, is quite apparent in *Sitophilus granarius* Linn., and *Sitophilus oryzæ* Linn., in their reactions to outer stimuli. The following notes constitute a summary of observations made recently on the "reflex immobilization" of numerous specimens of these species, both of which were supplied to me by the kindness of Dr. William Moore.

Sitophilus granarius Linn.

The granary weevil, while crawling about over grains of corn, will not feign death if the grains are disturbed so as to touch the weevils only slightly. However, if the disturbance takes place persistently and with a little force, the death-feint occurs. And it takes place instantly when the weevils are touched with the tip of a pencil, or a pair of forceps. These weevils, which have only vestiges of wings, appear to be quite sensitive to mechanical stimuli.

The death-feint posture is unlike that of death. In general, the following attitude is assumed. The first pair of legs extends anteriorly close to the body and parallel to the head. tennæ are also parellel with and close to the beak. The femora of the second pair of legs extend diagonally anteriorly, with the femora, tibiæ and tarsi folded upon each other. The femora of the third pair of legs extend posteriorly diagonally, with the femora, tibiæ and tarsi folded upon each other. The legs are all held close to the body. Sometimes the femora, tibiæ and tarsi of the first pair of legs are folded upon each other instead of being stretched out. Sometimes the antennæ stick out at various angles. And sometimes the legs do not all assume the rigid and fixed positions outlined above, but stick out grotesquely, or assume somewhat different positions. Apparently the intensity of the outside stimulus is important in determining the degree of rigidity.

The death-feint response in *S. granarius* may be brought about by various mechanical stimuli, such as turning the specimen over on its back, by picking it up with fingers or forceps, by dropping it from a height of two or three inches, by picking it up by one of its legs, by touching it almost anywhere on its body, although its dorsal surface is not so sensitive as its ventral one, by breathing upon it, by squeezing the antennæ and snout together, by pressing upon the ventral surface of the thorax, by pressing the sides of thorax and sometimes by vibrating the medium upon which it is resting. As a rule, death-feints, when the specimens were on their backs, lasted longer than when they were on their ventral surfaces, but there were many exceptions to this generalization.

The termination of the death-feint may be gradual or sudden. Usually the antennæ move first, then the first pair of legs and then the remaining pairs. In a gradual termination this sequence is easily observable. In a sudden termination, the recovery movements of these appendages appear to take place simultaneously.

During the course of the observations, the relative humidity varied from 36 to 40 per cent, the daylight or brightness from 4 to 150 candles per square foot, as measured by a Weston Photronic Exposure Meter, and the temperature from 68° F., to 94° F. As the relative humidity was almost constant, no further reference will be made to it. The brightness of the field in which the death-feint reactions were noted may also be neglected. cept for an instance of brightness approaching 150 candles per square foot, with a temperature of 73° F., the observations were made in fields where the brightness ranged from 4 to 65 candles per square foot, and this range will be immediately recognized as rather low. In all cases the degrees of brightness as noted appeared to have no effect upon the duration of the death-feint or upon the behavior of the insects. Temperatures, however, influenced the duration of the death-feint, as will be shown.

In the following Table I, there is shown the average duration in seconds of successive death-feints at various temperatures, of twenty-six weevils. The interval between the death-feints was approximately five seconds in duration. The longest number of successive death-feints was 104, after which the weevil refused to react. There was considerable variation in the duration of individual death-feints but the general tendency was for the death-feints to become shorter as they successively increased in numbers. It may be noted in Table I that as the temperature became higher the average duration of the death-feints declined. At temperatures of 88° F., and above, many weevils refused to feign death at all. The death-feints that did occur were short and recovery was rapid. Many refused to perform after two or three successive death-feints lasting a second or two. When the

TABLE I

AVERAGE DURATION OF SUCCESSIVE DEATH-FEINTS OF SITOPHILUS GRANARIUS

AT VARIOUS TEMPERATURES

Temperature in degrees F.	Number of successive death feints	Average (arithmetic duration in seconds
68	48*	15
68	· 72*	27
68	49*	58
70	21	38
70	16	34
70	14	29
70	18	36
70	11	40
72	104*	11
72	52*	23
73	11	35
73	4	37
74	48*	18
80	19	7
80	16	15
80	16	19
80	18	25
88	12*	6
88	29*	11
88	5*	3
88	2*	2
88	3*	1
94	2*	1
94 '	27*	4
94	6*	2
94	2*	2

^{*} Indicates termination of death-feints.

death-feint was induced at a low temperature, it was ended immediately when the weevil was placed under the influence of the higher temperatures.

In view of the variation in the duration of successive death-feints the average time in seconds does not show how long or short some of the death-feints lasted. This omission is supplied in Table II. Depending upon the temperatures the death-feints lasted from one to as many as 207 seconds.

TABLE II

RANGE IN DURATION OF SUCCESSIVE DEATH-FEINTS OF SITOPHILUS GRANARIUS

AT VARIOUS TEMPERATURES

Temperatures in degrees F.	Range in seconds
68	1 to 60
68	2 '' 80
68	2 " 207
70	3 to 118
70	4 ' ' 140
70	5 ' 65
70	5 ' ' 122
70	4 '' 95
72	1 to 71
72	2 '' 79
73	11 '' 100
73	25 '' 59
74	1 '' 56
80	1 to 14
80	4 ' ' 29
80	4 ' ' 45
80	7 ' ' 89
88	1 to 10
88	2 '' 27
88	1 '' 7
94	1 to 2
94	1 '' 6
94	1 ' 4
94	1 '' 2

The frequency distribution of the variations in the length of the death-feint at different temperatures is shown in Table III. At a temperature of 68° F., most of the recorded death-feints lasted from 1 to 30 seconds. Many longer death-feints occurred at this temperature but they were comparatively infrequent. At 72° F., most of the death-feints endured from 1 to 20 seconds, and at temperatures of 88° F., and above, the durations were from 1 to 10 seconds. Although the figures in Table III present some inconsistencies and do not indicate a fixed rate of progression from long to short death-feints as the temperatures increased, they do show that there is some correlation between the factors involved.

It is my belief that the variations in the durations of the deathfeints, within certain temperature groups (except 88° and 94°) are due principally to variations in the intensities of the outside stimuli. It is impossible, without special apparatus, for an experimenter to apply mechanical stimuli, time after time, that do not vary in intensity. During the course of the work, it was

TABLE III

FREQUENCY DISTRIBUTION OF VARIATIONS IN THE DEATH-FEINT DURATIONS OF
SITOPHILUS GRANARIUS AT VARIOUS TEMPERATURES

Length of death-feint	Temperature in degrees F.							
in seconds	68	70	72	73	74	80	88	94
1–10	30	13	72	0	15	24	37	37
11-20	34	11	39	2	16	28	10	
21-30	38	18	23	8	7	9	4	
31-40	19	11	13	1	8	3		
41-50	17	5	3	1	1	4		
51-60	13	9	2	2	1	0		
61-70	4	4	2	0		0		
71-80	7	1	2	0		0		
81-90	1	1		0		1		
91-100	0	2		1				
101-110	1	1						
111-120	1	1						
121-130	2	2						
131-140	1	1						
141-150								
Over 150	1							

noted that long death-feints seldom resulted from slight stimulations. On the other hand, deliberate rough treatment such as pinching the front legs and beak together very firmly, frequently resulted in death-feints of comparatively, long duration. In such cases the appearance of the weevil, with its legs drawn tightly to its body, indicated that the muscles controlling locomotion were in a tight state of contraction. As this state involved the antennæ also, the "hypnosis" probably extended throughout the nervous system. When the stimulus was slight, the muscular contraction was frequently not strong enough to draw the legs close to the body and they stuck out, sometimes at various angles. In most of these cases the death-feint was short and recovery was rapid, although in a few instances such "weak" death-feints lasted fairly long.

In order to determine how long a death-feint would last under prolonged stimulation, fifteen weevils were induced to feign death, and were then continually stimulated by being moved around and by pressure applied to the ventral surface of the thorax by the tip of a pencil or a pair of forceps. The durations of these death-feints in seconds at a temperature of 70° F., were 170, 300, 120, 28, 99, 434, 630, 635, 290, 1,290, 847, 2,160, 916, 434, 420, 384. The shortest was 28 seconds and the longest 2,160 seconds, or 36 minutes. The average length of the death-feint for the 15 individuals was 591 seconds, or almost 10 minutes.

Sitophilus oryzæ

Rice weevils in infested grain crawl over each other and allow parasites to crawl over them, seemingly without any desire to feign death. However, if touched by something foreign, deathfeints occur, but they are of short duration. On the whole this species does not seem as sensitive to outside stimuli as the granary weevil.

In the death-feigning attitude, the distal ends of the femora of the first pair of legs extend forward diagonally and are pressed against the base of the head. The femora of the second pair of legs extend forward diagonally and are held close to the body. The femora of the third pair of legs extend posteriorly diagonally, close to the body. In all cases the femora, tibiæ and tarsi are

folded upon each other, and held close to the body. The antennæ are parallel and close to the beak. In some cases the femora of the second pair of legs extend diagonally, posteriorly instead of anteriorly. Sometimes the antennæ participate only slightly in the muscular tension and do not assume a rigid attitude close to the beak. Frequently the tibiæ and tarsi are not folded close to each other but extend at wide angles from each other, although held close to the body. In other cases the legs stick out horizontally from the body. The death-feints of the rice weevil are comparatively brief. While assuming the death-feint readily if placed on their backs and with pressure applied to the thorax. they recover quickly. If handled and stimulated a few times they refuse to do anything except make efforts to escape. They are not very sensitive to outside stimuli. However, the deathfeint may be brought about by squeezing the sides of the thorax, by pressing against the ventral surface of the thorax, by squeezing the antennæ and beak together or by dropping the weevil from a height of one or two inches. If one method fails, frequently another one will succeed. In some cases individuals are even susceptible to a slight touch against the edge of the body. All in all, it is a difficult insect to work with, especially if the temperature is 75° F., or above, and many individuals refuse to feign death at this and even lower temperatures, except when squeezed or pressed quite hard.

During the observations with the rice weevil, the same relative humidity, light and temperature conditions prevailed as were recorded for *S. granarius* and the same conclusions apply to both species.

Table IV shows the average duration in seconds, of successive death-feints at various temperatures of twenty-four rice weevils, the interval between death-feints having been approximately five seconds. The longest number of successive death-feints was 29, after which the stimulus no longer produced a reaction. Individual death-feints varied considerably but the tendency was for the duration to decline as the number of successive death-feints increased. This table also shows that as the temperature increased, the death-feints became shorter. At a temperature of 74° F., and above, many individuals refused to feign death at

all. When they did, the attitude of the legs was not tense; they were not held close to the body, and recovery was rapid.

TABLE IV

AVERAGE DURATION OF SUCCESSIVE DEATH-FEINTS OF SITOPHILUS ORYZÆ AT

VARIOUS TEMPERATURES

Temperature in degrees F.	Number of suc- cessive feints	Average (arithmetic) duration in seconds		
68	16*			
68	22*	12		
68	8*	4		
68	9	4		
72	8*	4		
73	8*	3		
73	9*	12		
73	3*	2		
73	5*	4		
74	12	7		
74	17*	13		
74	6*	6		
80	3	1		
80	5	2		
80	29*	6		
80	3	1		
88	24*	4		
88	2*	1		
88	2*	1		
88	4*	2		
88	3*	1		
94	10*	3		
94	9*	2		
94	2*	1		

^{*} Indicates termination of death-feints.

Tables V and VI deal with the range in duration of successive death-feints and with their frequency distribution with relation to various temperatures. Death-feints lasted from 1 to 40 seconds depending upon the temperature and the greatest number of them took place within the range of from 1 to 5 seconds. As with the granary weevil, it is believed that the variations in durations of the death-feints in Sitophilus oryzæ, within certain temperature groups are due principally to variations in the intensities of outside stimuli.

TABLE V

RANGE IN DURATION OF SUCCESSIVE DEATH-FEINTS OF SITOPHILUS ORYZÆ AT

VARIOUS TEMPERATURES

Temperature in degrees F.	Range in seconds
68	1 to 12
68	2 " 7
68	1 ' ' 10
68	1 ' ' 10
72	1 ' ' 10
73	1 ' ' 13
73	2 44 2
73	5 ' ' 40
73	1 '' 6
74	1 '' 36
74	1 '' 11
74	2 '' 19
80	1 " 2
80	1 " 4
80	1 ' 20
88	1 " 9
88	1 " 3
88	1 " 2
94	1 " 5
94	1 '' 3
94	1 " 1

TABLE VI
FREQUENCY DISTRIBUTION OF VARIATIONS IN THE DEATH-FEINT DURATIONS OF SITOPHILUS ORYZÆ AT VARIOUS TEMPERATURES

Length of death-feint-	Temperature in degrees F.						
in seconds	68	72	73	74	80	88	94
1-5	27	6	15	15	28	29	21
6-10	13	2	6	9	9	6	
11–15	4		2	3	1	•	
16-20	9		1	4	2		
21-25	1		0	1			
26-30	1		0	0			
31-35			0	2			
36-40			1	1			

Under continued stimulation at a temperature of 70° F., only a few could be induced to prolong their death-feints. Seven weevils, stimulated continuously, remained immobile for the following numbers of seconds before recovering: 33, 19, 40, 11, 26, 3 and 75. The average time was 34 seconds.

Although Sitophilus granarius and Sitophilus oryzæ behave similarly in their reactions to contact stimuli under different temperatures, there is a great difference in the durations of their death-feints. In granarius it is brought about more readily and the locomotion reflexes are inhibited for a greater length of time. Both species exhibited the same nervous excitability after continued contact stimuli had brought about a condition in which the death-feint was no longer produced. And in high temperatures the reflex avoiding reaction took precedence over the "instinct" to feign death.